LIFE HISTORY OF CORALLINA OFFICINALIS VAR. MEDITERRANEA[1]

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The group of red seaweeds known as the Cryptonemiales includes many species displaying a wide variety of form. The structure of the reproductive organs and the mode of reproduction found in this group cannot be ascertained adequately by the study of a single species. In order to distinguish the Cryptonemiales from the other groups of Florideae, the method of reproduction, as existing in *Dudresnaya*, has constantly been cited as characteristic and representative of the entire group; but it is merely characteristic of that genus. Moreover, our present knowledge of *Dudresnaya* is confined to its morphological features. In any systematic arrangement of the forms belonging to the ill-defined Cryptonemiales, *Corallina* should always be placed near the summit. This does not mean, however, that the structure of the reproductive organs and the mode of reproduction are more complicated than in other forms belonging to this group. About 30 years ago, SOLMS-LAUBACH published his original work on the structure of *Corallina*, but no cytological work was attempted, and the life history of the plant was not established. Consequently, a cytological study of *Corallina* was made from material secured at the Bay of Naples, Italy.

Origin of conceptacle

Generally the conceptacles are formed at the ends of branches of the thallus. The reproductive organs, which arise within the conceptacles, originate from these so-called disk cells which compose the central portion of the growing apex of each branch. The disk cells located at the periphery continue to divide and grow up around the reproductive organs, leaving only a small aperture or ostiole at the apex, thus forming the conceptacle. The three kinds

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of reproductive organs (antheridia, carpogonia, and tetraspores) are produced in conceptacles on three different individuals.

Nuclear division in vegetative cells

Nuclear division is very common among any of the vegetative cells, but is most conspicuous among the actively growing (disk) cells at the ends of the branches. The cell structure varies more or less according to the position of the cell, but as a rule the nucleus occupies the central portion of the cell. One or sometimes two large vacuoles are present, and also many chromatophores. The cytoplasm seems to be distinctly alveolar in structure. The nucleus in the resting condition contains one and sometimes three or four irregular nucleoli. The chromatin material, during the resting condition of the nucleus, consists of small granules scattered throughout the karyolymph. Upon approaching the period of nuclear division, the nucleus slightly enlarges, and the chromatin, which up to this time was in the form of granules, increases in amount and finally becomes organized into a definite number of chromosomes. The male and female individuals possess twenty-four chromosomes, while the tetrasporic individuals have forty-eight. The contents of the nucleolus gradually become decreased with the formation of the chromosomes, and when the chromosomes have arranged themselves in an equatorial plate, the nucleolus has completely disappeared.

In the prophase a small, granular, centrosome-like body makes its appearance at each of the two poles of the nucleus in the cytoplasm near the nuclear membrane. Within the nucleus spindle fibers are soon formed, originating from the centrosome-like body. The alveoli of the cytoplasm immediately surrounding this centrosome-like body form branched astral rays. In later prophase the centrosome-like body becomes enlarged, and thus the centrosphere is produced.

In the metaphase the chromosomes divide, and when the two groups of daughter chromosomes reach the opposite poles, the daughter nuclei are soon formed. Up to and including the formation of the daughter nuclei, the centrosome-like body retains its characteristic form. With further growth of the daughter nuclei, however, it gradually decreases in size, and at the approach of the resting stage of the nuclei it becomes unrecognizable. With the return of the period of nuclear division, the centrosome-like bodies reappear, as just described, at the opposite poles of the nucleus.

SWINGLE and others who studied *Sphacelaria* and *Stypocaulon* maintain that the centrosome or "central body" persists from one mitosis to another. HARPER appears to be of the same opinion, as a result of his work on *Lachnea* and *Phyllactinia*. As regards *Corallina*, the two centrosome-like bodies appear for the first time at the period of nuclear division, and gradually disappear with the formation of the daughter nuclei. Thus these structures are not permanent organs of the cell, but arise *de novo* at each mitosis to carry on the mechanism of nuclear division.

Formation of tetraspores

By normal cell division the disk cell divides into two portions, the upper portion becoming the tetraspore mother cell, while the lower portion becomes the stalk cell. The tetraspore mother cell in its growth assumes a clavate form, while its nucleus increases in size. At first the structure of the nucleus appears to be the same as that of the vegetative nucleus, but by the time the conceptacle has developed sufficiently to be recognized as such, the nucleus of the tetraspore mother cell enters upon the stage of synapsis. In *Corallina* the chromatin material is so scanty that a continuous spireme cannot be formed, but remains in two groups of small granules at the poles of the nucleus. When the synaptic period has passed, a centrosome-like body appears at each pole. In the metaphase a group of twenty-four bivalent chromosomes becomes arranged in an equatorial plate, and the paired chromosomes split longitudinally and separate into two groups. The first nuclear division, which is the heterotypic division, is soon followed by the second, or homotypic division. With the completion of the second division, there are formed four nuclei within the tetraspore mother cell, each of which possesses twenty-four univalent chromosomes. Later the tetraspore mother cell, by means of three cleavage furrows, becomes divided into four portions, each of which develops into a tetraspore containing one nucleus. The tetraspores then escape from the conceptacle, float about freely in the water, and after becoming attached to a suitable substratum proceed to germinate.

Germination of tetraspores

The first nuclear division at the time of germination of the tetraspores shows twenty-four chromosomes. The same is true for the second and third divisions. With culture material the size of the plants obtained from germinating tetraspores was limited to thirteen cells. Throughout all these divisions there was no change as regards the number of chromosomes. The inference, therefore, is that such tetraspores, in nature, would give rise to sexual plants of normal size, possessing twenty-four chromosomes.

Formation of antheridium

The disk cell divides into two portions. The upper portion, which ultimately becomes the antheridium, is much smaller than the lower one, and is situated to one side of the latter. The two cells gradually become considerably elongated, the upper cell continuing to elongate until it finally attains a remarkable length. At the same time its nucleus divides, one daughter nucleus migrating to the extreme distal portion of the cell, while the other daughter nucleus remains in the lower portion. Just below the upper daughter nucleus a cell wall is formed, dividing the original upper cell into a very short terminal cell and a very long lower cell. The terminal cell becomes much enlarged and assumes a spherical form; the nucleus also enlarges greatly and occupies the larger portion of the cell. Thus the antheridium of *Corallina* is composed of a larger, spherical, terminal cell and a very much elongated, narrow, stalk cell. Later this spherical cell separates from the filiform stalk cell and functions as the spermatium. More than one antheridium may be formed from the same disk cell. The antheridial nuclei have constantly twenty-four chromosomes. The spermatium has a thin cell wall derived entirely from the mother cell, and when compared with other Florideae it is homologous with a unicellular antheridium. In 1911 SVEDELIUS, after having studied *Delesseria*, reported that the spermatium simply consists of the naked protoplast discharged from the mother cell. I believe, however, that this would be disproved by a careful reinvestigation.

Formation of procarp

Each disk cell produces one carpogonial branch or procarp. The steps in the development of the procarp are as follows: The disk cell divides to form two cells, the upper one becoming the auxiliary cell and the lower one the stalk cell. The auxiliary cell then gives rise to a cell at one side of its exposed terminal portion, and then similarly to another cell at the other side. Thus two sister cells are produced from the auxiliary cell, situated side by side. Of these two cells, the first one formed has become greatly elongated by the time the second sister cell is formed. The nucleus of the older sister cell divides to form two nuclei; one nucleus remains in the enlarged basal region of the cell (carpogonium) and becomes the carpogonial nucleus, while the other one enters the hairlike upper portion of the cell (trichogyne) and functions as the trichogyne nucleus. The trichogyne is separated from the carpogonium by a constriction. The younger sister cell, which is usually provided with one nucleus, ceases to grow further at an early stage in its development, and simply remains as a non-functional structure beside the carpogonium formed by its older sister cell. Every one of the many disk cells, at the growing tips of the thallus branches, produces a procarp.

As just described, each procarp is composed of a stalk cell, auxiliary cell, carpogonium, and trichogyne, together with the small non-functional sister cell of the carpogonium. The structure of the procarp of *Corallina*, therefore, would seem to be simpler than that of other Florideae; yet in many Florideae the procarps are solitary, or, as in the case of *Ceramium*, two occur side by side. In *Corallina*, however, 60–70 or sometimes over 100 independent procarps occur in a group within the same conceptacle, and after fertilization, before the formation of the carpospores, they fuse with one another, resulting in the formation of one common structure.

Fertilization and formation of cystocarp

The trichogynes project above the surface of the conceptacle and are thus freely exposed to the sea water. A floating spermatium comes in contact with the apex of the trichogyne, adheres to it, and discharges its contents into it. The trichogyne nucleus now begins to disintegrate. The spermatium nucleus proceeds downward, finally reaching the carpogonial nucleus, with which it fuses. At this time the auxiliary cell unites with the auxiliary cells of adjacent procarps, resulting in the formation of a large central cell within the conceptacle. The passage between this central cell and the carpogonium broadens. The sporophytic or fertilized carpogonial nucleus now passes into the large central cell. Since the sporophytic nuclei of all the procarps within the conceptacle migrate into this central cell, there are therefore over 100 sporophytic and also about the same number of gametophytic or auxiliary cell nuclei included in this common cytoplasm. The two kinds of nuclei found in the central cell differ as regards their structure. The sporophytic nuclei are usually large, rich in chromatin, and possess forty-eight chromosomes; the gametophytic nuclei are small, possess twenty-four chromosomes, and most of them gradually disintegrate.

Each sporophytic nucleus moves to the periphery of the central cell, where it divides to form two nuclei. One nucleus enters the cell which has been formed on the outer surface of the central cell, while the other nucleus remains inside the central cell. From the cell produced on the external surface of the central cell, a chain of cells is formed in basipetal sequence. These cells enlarge, become spherical, and when they have attained the size of tetraspores, gradually become constricted, separate, and finally escape from the conceptacle as carpospores.

Germination of carpospores

After the carpospores have escaped from the conceptacle, they begin to germinate within twenty-four hours. The first nuclear division is of the normal type and shows forty-eight chromosomes. The same is true of the second and third divisions. The sporelings continue to develop until the 17-celled stage is reached, all of the cell divisions being of the normal type and showing constantly forty-eight chromosomes.

Summary

1. The male and female plants of *Corallina* possess twenty-four chromosomes, while the tetrasporic plants have forty-eight chromosomes.

2. During the formation of tetraspores the forty-eight chromosomes become reduced to twenty-four. The tetraspores on germination show twenty-four chromosomes, and since twenty-four chromosomes appear in the vegetative mitoses of the sexual plants, the inference is that the latter arise from tetraspores.

3. The nuclei of the reproductive cells (spermatia and carpogonia) of the sexual plants possess twenty-four chromosomes. The sporophytic or fusion nucleus, as a result of fertilization, has forty-eight chromosomes. The sporophytic nuclei give rise by division to the carpospores, which also possess forty-eight chromosomes. The carpospores on germination show forty-eight chromosomes, and since forty-eight chromosomes appear in the vegetative mitoses of the tetrasporic plants, it is inferred that the tetrasporic plants originate from carpospores.

4. The male and female plants are gametophytic, while the tetrasporic plants are sporophytic. The sporophytic generation begins with the formation of the sporophytic or fusion nuclei, extends through the formation of the cystocarp and carpospores, and finally terminates with the formation of tetraspores on the tetrasporic plant. With the formation of the tetraspores, the gametophytic generation commences.

5. Thus *Corallina* is another clear example of the alternation of a sexual plant (gametophyte) with a tetrasporic plant (sporophyte), the cystocarp occurring as an early phase of the sporophytic generation.

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